THE QUESTION OF THE PHYLOGENETIC ORIGIN OF TERMITE CASTES.

CAROLINE BURLING THOMPSON[1] AND THOMAS ELLIOTT SNYDER.[2]

It has recently been shown by one of the authors (C. B. T.) that the ontogenetic origin of the castes of the termite *Reticulitermes flavipes* Kol., formerly *Leucotermes flavipes*, is due to intrinsic causes, and not to the extrinsic stimuli which have long been credited with formative, indeed almost creative powers. Grassi (1893–94) and his followers described the plastic, "undifferentiated," newly hatched nymphs, upon which the action of the stimuli of food, parasites, fraternal care, etc., wrought out the highly differentiated adult castes. In favor of Grassi's hypothesis is the fact, that, in most genera, the newly hatched termite nymphs, about one millimeter long, are externally all alike. On the other hand, Grassi's hypothesis is disproved by the recent observations that termite nymphs are already differentiated at the time of hatching (Bugnion, 1912–'13, Thompson, 1917).

Bugnion states that, at the time of hatching, the soldier (nasutus) caste of the termite *Eutermes lacustris* Bugn. is sharply differentiated from the other nymphs by external structural characters. He has not worked out the differentiation of the other castes, which is, of course, a simple matter of observation, but his general conclusion, based upon this and other investigations, is that the castes of *Eutermes lacustris* originate in the embryonic period, and that the cause of differentiation is deep seated, and probably analogous with the cause of sex (Bugnion, 1912, '13).

Thompson (1917) finds that in *Reticulitermes flavipes* the newly hatched nymphs are externally all alike, but are differentiated by internal structural characters into two clearly defined

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types, the reproductive and the worker-soldier types, which give rise, respectively, to the three adult reproductive castes and the two adult sterile castes. The two types of newly hatched nymphs are distinguishable by four structural characters: the

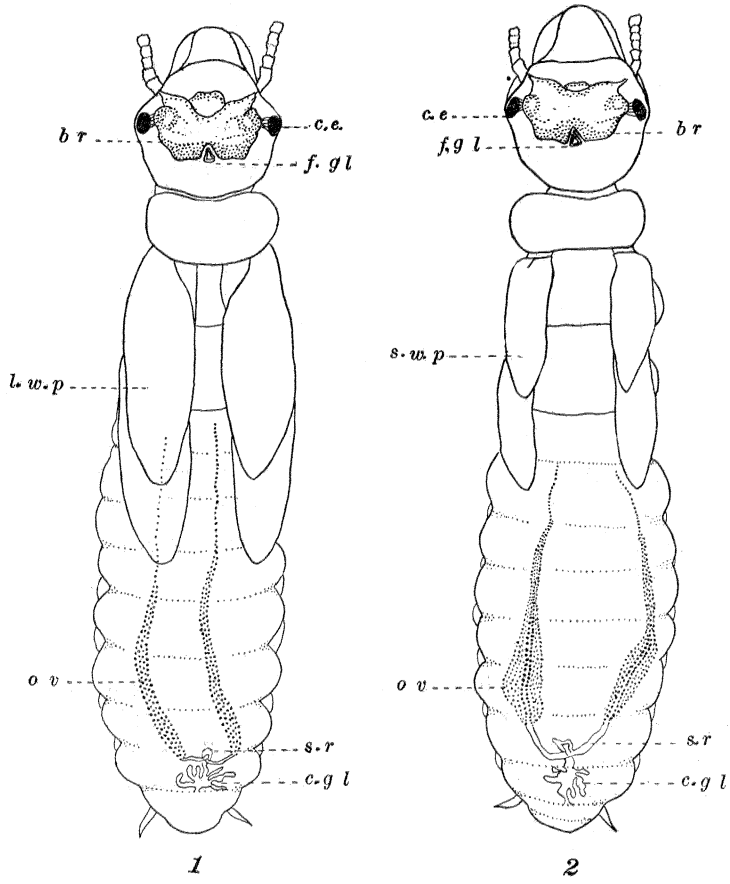

FIG. 1. *Reticulitermes flavipes*. Female nymph of the first form, drawn from a whole mount.

FIG. 2. *Reticulitermes flavipes*. Female nymph of the second form, drawn from a whole mount. The ovaries, *ov*, which in their later development, are of secondary size, are now more swollen than in the nymph of the first form, since the ova of the second form nymphs mature at an earlier age. For the relative size of the ovaries of mature queens of the first and second forms, compare Figs. 6 and 7. It should be noted that all the parts of the reproductive system are fully formed and connected in these two fertile nymphs.

Br, brain; *c.e*, compound eye; *c.gl*, colleterial gland; *f.gl*, frontal gland; *l.w.p*, long wing pad; *s.w.p*, short wing pad; *s.r*, seminal receptacle; *ov*, ovary. Oc. 6, obj. 32 mm., drawn at stage level. Reduced one third. Drawn by C. B. T.

bulk of the brain, the relative size of brain and head, the compound eyes, and the sex organs. When the young reproductive nymphs have attained a length of 1.3–1.4 mm. other structural differences are observable that further differentiate them into two kinds of individuals which later develop into two of the three adult reproductive castes, namely: adults of the first form, with long wings, and adults of the second form, with short, scale-like wing pads. The ontogeny of the third adult reproductive caste, without wing stubs or wing pads, is yet to be worked out in *R. flavipes*. At a later period in the ontogeny—body length about 3.75 mm.—the worker-soldier nymphs differentiate into two kinds of nymphs which develop into the two sterile adult castes, the workers and the soldiers.

As a result of the discovery that the ontogenetic cause of termite castes is intrinsic, two questions arise. First, can this intrinsic ontogenetic cause be determined by cytological means, *i. e.*, by examination of the phases of ovogenesis and spermatogenesis? Second, what is the phylogenetic origin of the termite castes? It is with this second question that the present paper deals.

The phylogenetic mode of origin of the castes of termites, could it be determined, might have an important bearing upon the general question of the evolution of species. The condition of polymorphism, or the existence of several structural forms within a species, indicates that the parent or ancestral form had a tendency to vary. Two categories of variations are recognized today: (1) the variations which have arisen abruptly and are qualitatively unlike the parent condition, and which breed true to type,—"sports" of Darwin, "mutations" of DeVries, "discontinuous variations" of Bateson; (2) the "fluctuating" variations which have arisen gradually and are merely quantitative variations of the parent condition—"Darwinian variations," "fluctuations" of DeVries, "continuous variations" of Bateson. It is well known that the selectionists claim that the latter type of variation is heritable[1] while on the other hand the mutationists and the pure line school either doubt or deny that fluctuating variations are inherited.

[1] Castle (1917); Jennings (1917).

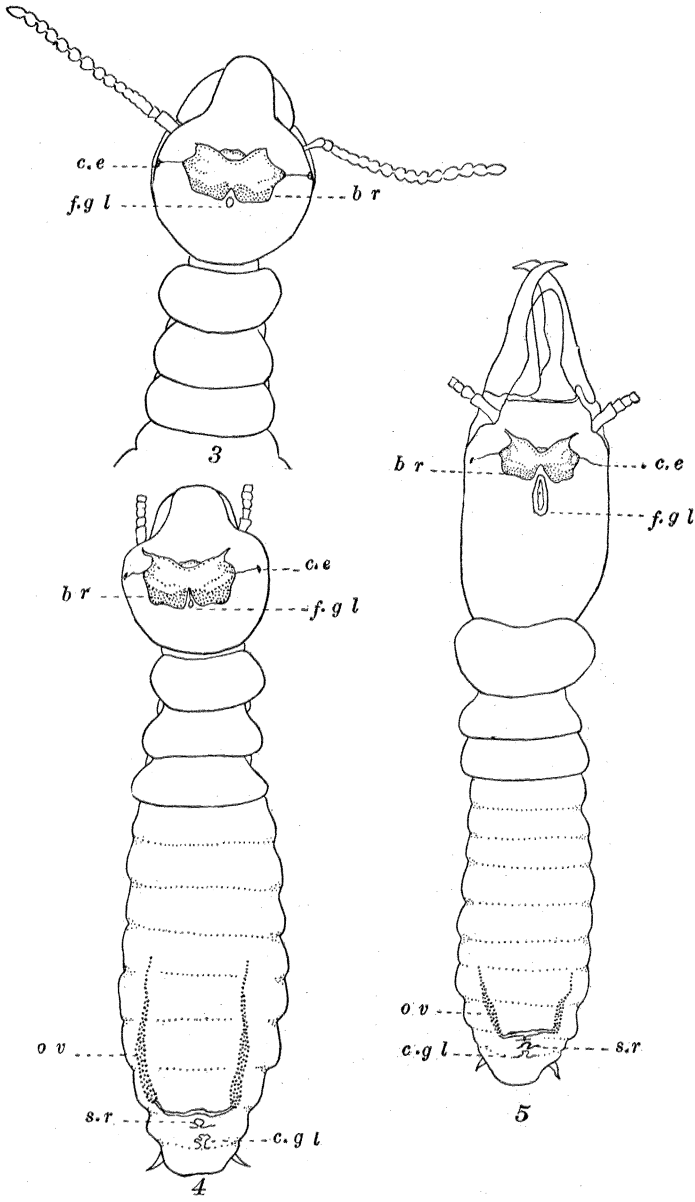

FIG. 3. *Reticulitermes flavipes*. Mature queen of the third form, head and thorax, drawn from a whole mount.

FIG. 4. *Reticulitermes flavipes*. Female worker, adult, drawn from a whole mount.

FIG. 5. *Reticulitermes flavipes*. Female soldier, adult, drawn from a whole mount. It should be noted that the parts of the reproductive system are separate and in an embryonic condition in the sterile workers and soldiers, Knower (1901).

Br, brain; *c.e*, compound eye; *c.gl*, colleterial gland; *f.gl*, frontal gland; *s.r*, seminal receptacle; *ov*, ovaries. Oc. 6, obj. 32 mm., drawn at stage level. Reduced one third. Drawn by C. B. T.

The question that presents itself to our minds is, therefore, in which of these two categories of variations do the termite castes belong? or, in other words, are the castes of termites, both in origin and at present, to be considered as fluctuating variations or as mutations?

Several lines of approach lead toward the solution of this problem: (1) the study of fossil insects, from the Cretaceous period when termites are said to appear[1] up to the present time; (2) the comparative morphology of the order of termites; (3) exact field observations upon termite biology; (4) breeding experiments to determine the type of progeny and the results of hybridization.

None of these lines of work have been thoroughly or exhaustively investigated, and the gaps in our knowledge are very wide. There are, however, a few scattered observations, to be summarized in this paper, drawn partly from the literature of the social insects, and partly from the field and laboratory studies of the two authors, which may be of value in the attempt to solve the problem of the variations known as termite castes.

In a recent paper, Wheeler (1917) has stated his opinion that the castes of ants represent continuous, *i. e.*, fluctuating variations. This view is based upon the study of the fossil ants of the Baltic amber, and upon comparative morphological data. "In most species of ants the constant and striking structural differences between the different castes would, at first sight, suggest that such forms as the apterous females, apterous males, soldiers and workers, must have arisen as so many saltatory variations, or mutants and that they survived and secured representation in the germ-plasm, because they happened to fulfill specialized and useful functions in the life of the colony. I believe, however, that this view of the castes, at least so far as their origin is concerned, cannot be maintained, because all the available evidence points to their being merely the surviving extremes of graduated and continuous series of forms, the annectant members of which have suffered phylogenetic suppression or extinction."

Handlirsch (1908), p. 1191, states that the number of termite genera was far greater in the Tertiary period than at present.

[1] Handlirsch (1908).

The field of termite morphology needs much revision, but a few significant facts may be stated here.

TABLE I.

THE CASTES OF *Reticulitermes flavipes* KOL.

Reproductive castes.	1. Adults of the first form.....	Long wings, or stubs after deälation; brain, compound eyes, and frontal gland large; mature sex organs largest of any caste; abundant pigment in skin. Aërial habit of swarming.
	2. Adults of the second form...	Short wing pads; brain, compound eyes, and frontal gland smaller; mature sex organs slightly smaller; less pigment. Subterranean mode of life.
	3. Adults of the third form.....	Entirely wingless; brain small, compound eyes, and frontal gland vestigial; mature sex organs much smaller; still less pigment. Subterranean mode of life.
Sterile castes.....	4. Workers.....	Wingless; brain small, compound eyes and frontal gland vestigial; sex organs embryonic; no pigment in body. Subterranean mode of life. Head broader than in the first and second reproductive forms, stouter mandibular muscles.
	5. Soldiers.....	Wingless; brain very small, compound eyes vestigial, frontal gland large; sex organs embryonic, even smaller than in the worker; no pigment in body. Subterranean mode of life. Elongate head, long mandibles, massive mandibular muscles.

An examination of the five castes of *R. flavipes* (Figs. 1–5, 6–8, 13–15, and Table I) shows that a gradation of characters may be traced throughout the series. In the three reproductive castes (Figs. 1, 2, 3), beginning with the winged adult of the first form, or its nymph of the first form which is practically similar in structure, an increasing loss of size is to be noted in the wings, in the brain, compound eyes, and frontal gland, and in the sex organs. The darkly pigmented body and the aërial habit in swarming are found only in the adults of the first form, less pigment and a wholly subterranean mode of life in the second and third forms. In the case of the worker (Fig. 4), and to a greater extent in the soldier (Fig. 5), there is a gain as well as a loss of characters, the gains being manifested in the larger head, pigmented in the soldier, and the larger mandibles and mandibular muscles; the losses, in the body pigment, the wings, brain, compound eyes, and sex organs. The frontal gland is merely vestigial in the worker, but is highly developed in the soldier. These castes might be interpreted either as gradations in a series of continuous or fluctuating variations, or as a series of regressive mutations, *i. e.*, mutations formed by the loss of characters, comparable to the series of mutations found in *Drosophila*, Morgan et al. (1915), Morgan and Bridges (1916). Should the former prove to be the case, then transitional or intermediate forms between the existing castes should be expected, but it must be remembered that mutations also may be arranged to form a structural series, even though they may not have originated in this order.

Up to the present time rather few intermediate forms have been described. The reason for this may be either that they have been overlooked thus far, or that they do not exist. The intermediate forms known at present are as follows:

In colonies of *Termopsis angusticollis* Walker, Heath (1903) describes fertile soldiers with wing buds, which produced "normal progeny." The question might well be asked what would be "normal progeny" under these circumstances?

Soldiers with vestiges of wing pads have been noted by the two authors in several species of *Calotermes: C. occidentis* Walker, and two new species from southern Florida; and by N. Banks in

TABLE II.

Genus.	Reproductive Castes.			Sterile Castes.			Variations.
	With Long Wings.	With Short Wing Pads.	Wingless.	Worker.	Soldier.	Nasutus.	
Termopsis Heer.....	1st form.	Forms with shorter wing pads than the normal 2d form.	3d form.		Soldier.		
Calotermes Hag.....	1st form.	2d form.	3d form.		Soldier.		*Calotermes* n. sp. from Fla., soldiers with abnormally shaped heads.
Neotermes Holm.....	1st form.	[2]	[2]		Soldier.		
Cryptotermes Bnks	1st form.	[2]	[2]		Soldier.		
Reticulitermes Holm.....	1st form.	2d form. (Also forms with both shorter and longer wing pads than the normal 2d form.)	3d form.	Worker.	Soldier.		*Reticulitermes* n.sp. from Pacific Coast, soldiers with longer heads.
Arrhinotermes Wasm	1st form.	2d form nymphs have been found, but no adults.	3d form.	Worker.	Soldier.		
Hamitermes Silv.....	1st form.	2d form.	[2]	Worker.	Soldier.		
Anoplotermes F. Müll. ..	1st form.	2d form.	[2]	Worker.			
Eutermes F. Müll.....	1st form.	2d form (in tropical species).	3d form (in tropical species).	Worker.		Nasutus.	

[2] This caste may exist in nature but it has not yet been found.

C. minor Hagen, and other species of *Calotermes*. Vestigial wing pads are evidently of frequent occurrence in this genus although these soldiers are in general not fertile.

The Rev. F. L. Odenbach, S.J., of Cleveland, Ohio, has kindly loaned his manuscript notes from which we quote. In one of Odenbach's colonies of *Reticulitermes flavipes*, an enlarged egg-laying queen, figured in manuscript notes and referred to by Snyder (1915, p. 56), has the abdomen distended and the abdominal tergites separated, but possesses long, well developed wing pads like a nymph of the first form.

Grassi (1893) has figured a queen which, in respect to the length of the wing pads, is an intermediate between the first and second forms in the species *R. lucifugus* Rossi.

Another peculiar form has been found in a colony of *Reticulitermes* n.sp. from Montana. This specimen (a male) has the head heavily chitinized and yellow in color as in the soldier; the mandibles and labrum are like those of the worker; but the head is slightly more elongate than the typical worker head. The total length of the specimen is nearer to that of the soldier. Unfortunately the antennæ are broken, so that the question whether it is a worker or soldier can not be determined from the number of segments. After staining, the frontal gland, the compound eyes, the brain, and the sex organs were identified as those of the worker caste (see Table I.). This specimen is evidently only a worker of abnormal development, and not, as was first thought, an intermediate form between the worker and the soldier.

An argument against the view that the termite castes are mutations is the fact that the five castes are constant in their structural characters and more or less constant in their occurrence throughout the very different and widely distributed genera of the three families of termites. In the native American genera listed in Table II. the first form or reproductive adult with long wings is found in every genus. Either a second or a third form adult is probably of similar occurrence. Sometimes both are present, sometimes one or the other is said to be lacking. This may be a real absence of the caste in question, or it may be due to incomplete field data. There is no worker caste in the primitive

genera *Termopsis* Heer, *Calotermes* Hag., *Neotermes* Holmg., and *Cryptotermes* Banks, but the activities of workers are carried on by the nymphs of the reproductive forms.

There is no soldier caste in the genus *Anoplotermes* Fritz Müller; this caste is also lacking in the genus *Eutermes* Fritz Müller, but here a new sterile caste has appeared: the "nasutus," a soldier-like form with a prolonged frontal process or "beak," which is often erroneously termed a soldier.

Many tropical species of termites have two types of soldiers and workers occurring within the species. The differences, however, are not marked structural ones but are quantitative, consisting mainly in the relative sizes of the two types, there being both "large" and "small" soldiers and "large" and "small" workers. These two types of worker or soldier or both, are said to occur in the genera *Rhinotermes* Hag., *Acanthotermes* Sjöst., *Termes* Linn., *Hamitermes* Silv., *Cornitermes* Wasm., *Eutermes* Fritz Müller, and *Leucotermes* Silv. In tropical species of *Eutermes* two types of nasuti, large and small, have been found. In our Nearctic termites, only two species have been seen with such differences in the soldiers. In two new species of *Calotermes* from Florida there are slight differences in the shape of the heads of soldiers *from the same colony*, and in *Reticulitermes* n. sp. from the Pacific coast there are also differences in the length of the heads of soldiers, but *from different colonies* (see Table II.).

Field Observations and Artificial Breeding Experiments.

With the collapse of the fantastic theories of Grassi and others in regard to the voluntary manufacture by the workers of "substitute" and "complemental" royal forms to replace the loss of the "true," winged, or first forms, we find ourselves at a loss to furnish the answer to the question how the different reproductive castes actually reproduce their kind today. Do the winged adults of the first form today give rise to the adults of the second and third forms as well as to the workers and soldiers? or does each fertile caste reproduce only its own fertile type together with the sterile forms?

Field observations upon species of the genus *Reticulitermes* by one author (T. E. S.) indicate that reproductive individuals

of the first form probably produce the nymphs of all three reproductive castes. At the proper season of the year—before the time of swarming—nymphs of the first and second forms are commonly found together in colonies, although colonies have been found in which no nymphs of the second form have been observed. Nymphs of the third form have never yet been found, which may be due to their resemblance to the young of the other castes; there is a possibility, however, that the individuals of the third form may be fertile workers, a point to be determined by morphological data, and now being investigated by one of the authors.

Both field observations and breeding experiments seem to indicate that the second and possibly the third forms produce, in addition to the sterile workers and soldiers, only their own fertile types, and never nymphs of the first form. In other words, the second and third form reproductive adults apparently breed true to their fertile types. In some artificial colonies with parent reproductive individuals of the second form, no reproductive forms but only sterile workers and soldiers have been produced. This seems to be the case in the two following experiments.

The Rev. F. L. Odenbach received in September, 1900, a small colony of termites, *Neotermes castaneus* Burm., from Florida. He placed these insects in an artificial nest and has continued to make observations on their habits. On July 1, 1902, eggs were found in the nest. In February, 1908, about one hundred and fifty members were present in the colony. In September, 1908, and again in June, 1909, reproductive forms were observed in the nest, much larger than the other members of the colony, and some with an enlarged abdomen, the body segments appearing as prominent chitinous bands, due to distention, a characteristic of the older termite queens. From Odenbach's description these were evidently reproductive individuals of the second or third form. In December, 1910, approximately two hundred individuals were in the nest. This colony was still alive in September, 1917. Workers and soldiers, but no forms with wing pads nor any winged adults, have been produced in this colony after seventeen years of breeding.

On August 2, 1915, one of the authors (T. E. S.) received a colony of a termite (*Reticulitermes* n. sp.) from Ivywild, Colo., found in a scrub white oak, and consisting of workers, soldiers and nymphs. On November 22, 1915, three females with abdomens considerably distended and two males with slightly distended abdomens were observed in the nest. These were reproductive individuals of the second form and had grayish and yellow pigmentation in the chitinized parts. While numerous eggs have been found every month in the year in this artificial colony, maintained indoors, and while the number of workers and soldiers has increased, no forms with wing pads or wings have been produced up to December, 1918, after three years of breeding, and the colony is large—several hundred members—and healthy. The criticism can scarcely be made that there has not been sufficient time for the production of winged forms, for even in recently established incipient colonies in nature the nymphs of the winged reproductive forms are produced after eighteen months.

Heath (1903) found winged adult termites of *Termopsis angusticollis* Walker swarming from nests in which males and females of the first form were present, the nests being only two years old and containing two hundred individuals.

One of the authors (T. E. S.) has made observations on the habits of termites since 1912, mainly in the southeastern United States, but in the season of 1917 during an extensive field trip through Florida, the southwest, the Rocky Mountains and the Pacific Coast regions. It may be stated with certainty that: (1) in long-established colonies, in which large fertilized queens of the second from occurred, no nymphs or winged adults of the first form have been found; (2) in all colonies in which queens of the third form were found, no nymphs or winged adults of the first form occurred; most of these colonies, however, were all small or young, that is, they had been recently established. In one large colony of *R. flavipes* in Virginia, with seventeen third form queens present, a few nymphs of the second form were found. Very few males of the third form have yet been found in the genus *Reticulitermes*, which is possibly due to their resemblance to young nymphs of the reproductive forms or to workers, and

to the fact that they are not so enlarged as the females. In the related genus *Arrhinotermes* males of the third form are of common occurrence.

The colonies of *Reticulitermes flavipes* and *virginicus* found in the southeastern United States in the spring, often contain nymphs of the second form, sometimes in large numbers, associated with either nymphs of the first form or winged sexual adults. These young reproductive types of the second form (Fig. 2) have attained their mature pigmentation at about the same time that the colonizing winged adults or reproductive types of the first form swarm, but after the swarm they are not found in the parent colonies. We may ask why they are produced and what becomes of them? They are not needed in the parent colony any more than the winged colonizing forms and it may be that they are impelled to leave the old colony by the same irresistible force that induces the swarm or flight. It may be, that, accompanied by workers and soldiers, they leave the parent colony by means of subterranean passages and establish a new colony. Since the origin of the castes is due to intrinsic causes, Thompson (1917), a certain proportionate number of these nymphs of the second form may be produced each year in long established colonies with parent first form adults. They would evidently be superfluous if the original reproductive forms of the parent colony were present, and might therefore be forced to migrate.

In certain colonies of termites, reproductive individuals of the second form occur with a small proportion of males to a large proportion of females. In the genus *Reticulitermes* as many as eight males together with thirty-two females, and fifteen males with twenty-eight females, both sexes of the second form, have been found (T. E. S.). In other colonies of *Reticulitermes* there are only reproductive individuals of the third form. Sometimes, again, a male of the first form is found with numerous (sixteen) mature females of the second form. Grassi would have described these second form females as "substitute" queens, produced by the workers to fill the place of a missing "true" queen.

It is an open question how they are to be accounted for with our present knowledge, and we have no exact data as to the

progeny. In one instance three queens of the third form and one queen of the second form were found together in the same colony, but both sexes of two different mature reproductive castes have never been found in one and the same colony of *Reticulitermes*. No experiments in crossing the different forms have yet been made.

The two authors hope to undertake a thorough investigation of the termite castes, especially of the three reproductive types, with an analysis of their breeding. This will be carried on by means of field and laboratory observations and by breeding experiments which will require several years to complete.

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DESCRIPTION OF PLATES.

FIGS. 6–9 are photographs of sections of the abdomens of termite queens. Figs. 10–12 are photomicrographs of the same sections made by John H. Paine, of the Bureau of Entomology. Figs. 13–15 are photographs of the living insects.

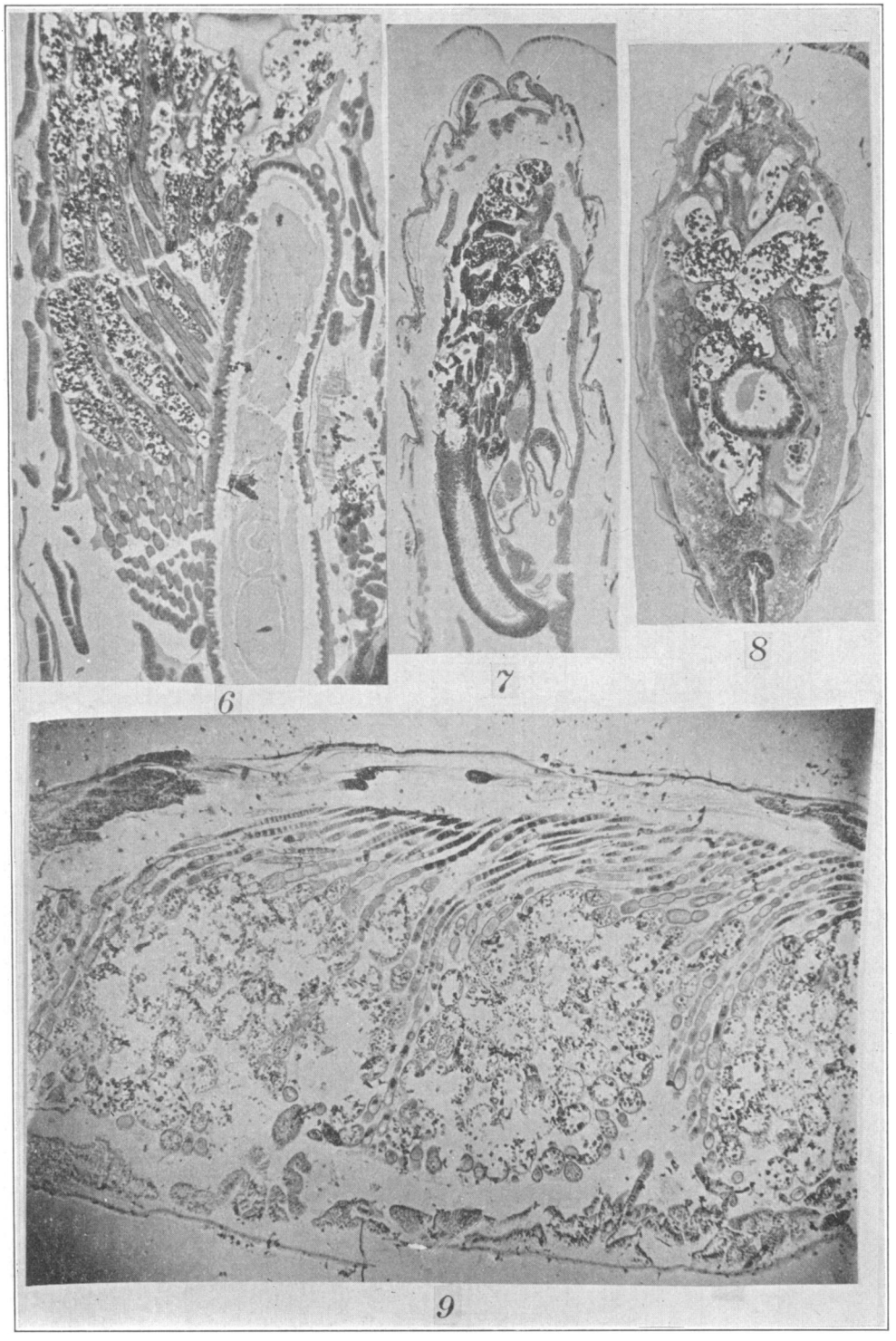
EXPLANATION OF PLATE 1.

FIG. 6. *Reticulitermes flavipes.* Photograph of a section of part of the abdomen of a mature first form queen, showing that the relative extent of the ovarian tubes is greater than in either of the other reproductive castes. × 20.

FIG. 7. *Reticulitermes flavipes.* Photograph of a section of the abdomen of mature queen of the second form. A portion of the oviduct is seen with the egg tubes opening into it laterally. × 20.

FIG. 8. *Reticulitermes flavipes.* Photograph of a portion of a section of the abdomen of a mature queen. The extent of the egg tubes is less than in the other two forms, but the ova shown happen to be of the oldest stage and are therefore larger. × 20.

FIG. 9. *Eutermes morio.* Photograph of a section of the abdomen of a mature queen of the first form, showing the enormous extent of the egg tubes and the varying sizes of the ova. × 20.



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EXPLANATION OF PLATE II.

FIG. 10. *Reticulitermes flavipes.* Mature queen of the first form, ovarian tubes. Photomicrographs of a portion of the same section shown in Fig. 6. × 65.

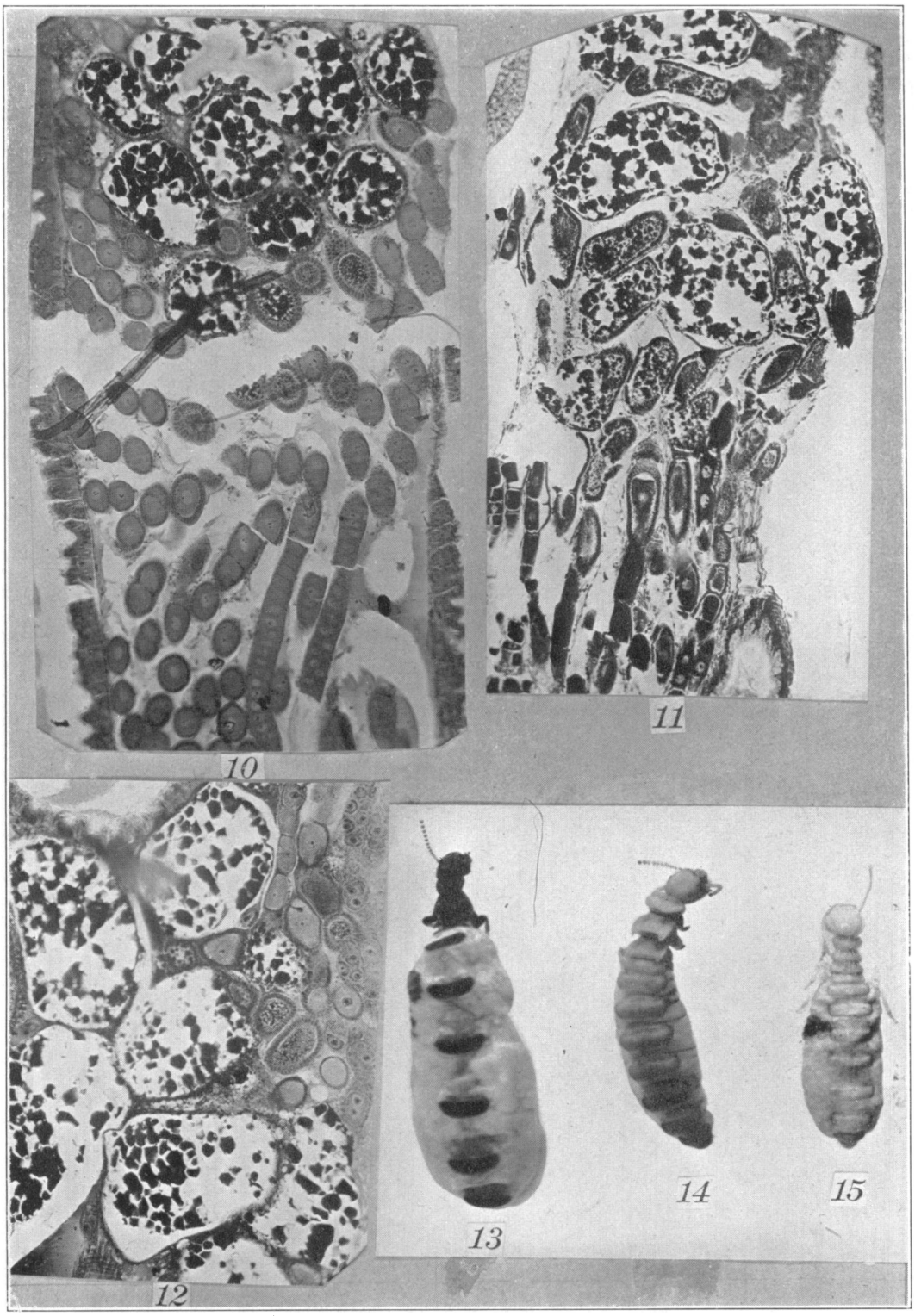
FIG. 11. *Reticulitermes flavipes.* Mature queen of the second form, ovarian tubes. Photomicrograph of a portion of the same section shown in Fig. 7. The oviduct and four entering egg tubes may be seen. × 65.

FIG. 12. *Reticulitermes flavipes.* Mature queen of the third form, ova. Photomicrograph of a portion of the same section seen in Fig. 8. × 65.

FIG. 13. *Reticulitermes flavipes.* Photograph of a mature queen of the first form. × 5.

FIG. 14. *Reticulitermes flavipes.* Photograph of a mature queen of the second form. × 5.

FIG. 15. *Reticulitermes flavipes.* Photograph of a mature queen of the third form. × 5.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